The Veliger 27(4):375-380 (April 1, 1985)

THE VELIGER

The Activity Pattern of *Onchidella binneyi* Stearns (Mollusca: Opisthobranchia)

by

PHILIP J. PEPE AND SUEANNE M. PEPE

Center for the Study of Deserts and Oceans, P.O. Box 53, Puerto Peñasco, Sonora, Mexico

Abstract. *Onchidella binneyi* inhabits the upper intertidal zone on rocky shores of the Gulf of California. At El Bajo, B.C.S., Mexico, the activity of a population of *O. binneyi* followed a distinct pattern. The nightly activity period began shortly after the ebbing tide exposed the animals' position on the shore. The number of active animals increased steadily to a maximum and then declined until all activity ceased during the hour of low tide.

The activity cycles of *Onchidella binneyi* were synchronous with the tides. The maximum number of animals active each night was inversely correlated with the tidal height at low tide. At neap tides the *O. binneyi* population was inactive. At spring tides the intensity of activity reached a maximum.

Animals were held in aquaria in a non-tidal simulation. They continued to exhibit daily activity very similar to the field population. This indicates that either the population is directly cued by some environmental factor that fluctuates in relationship to the tides, or that *Onchidella binneyi* possesses an internal biological clock.

INTRODUCTION

Onchidella is a small genus of opisthobranchs that has a wide geographical distribution. Members of this genus are completely shell-less as adults, with papillate mantles and lungs (WATSON, 1925; FRETTER, 1943). Their mantle margins contain repugnatorial glands whose secretions are effective against a wide range of possible predators including crabs and fish (AREY & CROZIER, 1921; WATSON, 1925; IRELAND & FAULKNER, 1978). *Onchidella* inhabits rocky shores, living in eroded cavities or clefts between stones (AREY & CROZIER, 1921; WATSON, 1925; FRETTER, 1943; MARCUS & MARCUS, 1956). With few exceptions, species of *Onchidella* have been reported only from the intertidal zone.

Activity patterns synchronous with ocean tides have been reported for four species of *Onchidella*: *O. verruculatum* Cuvier (HIRASKA, 1912), *O. floridanum* (Dall) (AREY & CROZIER, 1921), *O. celtica* (Forbes & Hanley) (FRETTER, 1943), and *O. indolens* (Gould) (MARCUS & MARCUS, 1956). In each case animals were observed crawling about on the top surfaces of rocks during daytime ebbing tides only. During other tidal stages, they were not observed on the surface of the rocks but were found inactive within rock cavities.

AREY & CROZIER (1921) observed *Onchidella floridanum* on Bermuda shores and reported a diurnal activity pattern for this species. *Onchidella floridanum* emerged from its rock shelters only after the falling tide had left it exposed to the air for approximately one hour. Individuals were observed actively grazing diatoms on the rock surfaces for an additional hour. After the grazing period, the animals simultaneously returned to their shelters. All animals had disappeared from the top surfaces of rocks before low tide.

Onchidella binneyi Stearns, 1893, a dark gray slug approximately 2.5 cm long, is endemic to the Gulf of California. Preliminary observations in May 1978 indicated that *O. binneyi,* although active only at night, had an activity pattern similar to that of *O. floridanum.* A study was designed to determine whether the activity of a population of *O. binneyi* was synchronous with ocean tides and whether the behavior would persist if animals were left in standing seawater in aquaria.

STUDY AREA

The study area was located at El Bajo, 10 km north of Loreto, Baja California Sur, Mexico, on the shore of the central region of the Gulf of California. At El Bajo the upper intertidal zone consists of densely packed basalt boulders and shingles over a sand base. The beach slopes

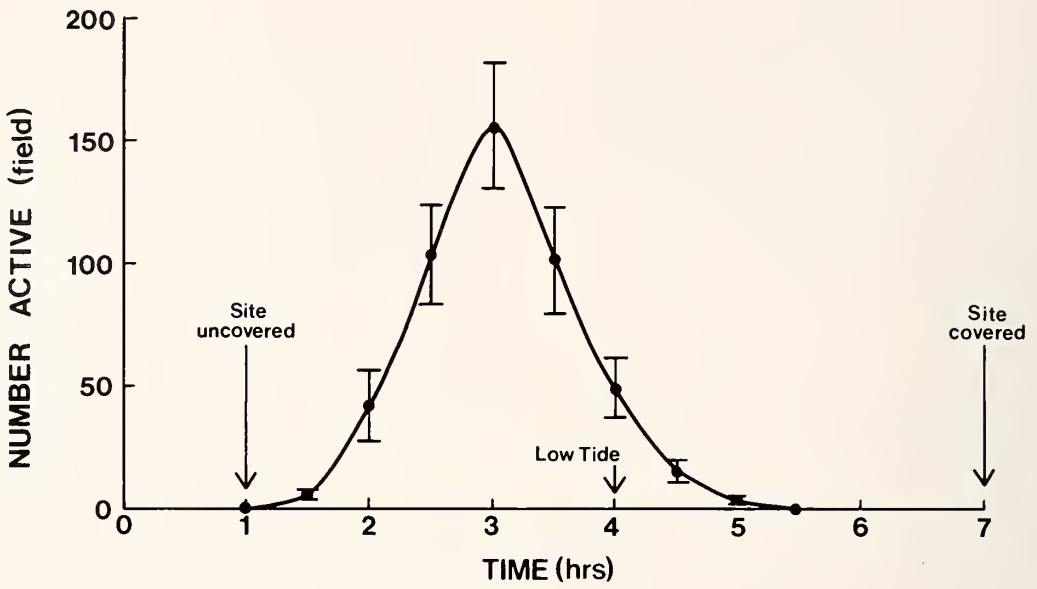

Figure 1

The mean number of active animals during 25 nights of activity for the *Onchidella binneyi* population at El Bajo, B.C.S., Mexico. The bars represent the standard errors of the mean. The arrows indicate the average time of the animals' exposure to the air and the average time of low tide relative to the activity of the population.

about 4° seaward. *Onchidella binneyi* lives in a narrow zone buried beneath the stones. This zone is located at a tidal height of approximately 0.8 m above mean lower low water (MLLW). El Bajo is protected from storm surge by a nearby offshore island, Isla Coronado.

The central region of the Gulf of California has mixed semi-diurnal tides that change to a diurnal pattern during the neap portion of a tidal series. At El Bajo the maximum tidal range is approximately 1.4 m. The tides at El Bajo match the NOAA predictions for Guaymas, Sonora, Mexico.

Onchidella binneyi lives just below mean sea level (MSL), or the break between the high and middle intertidal zones as defined by RICKETTS & CALVIN (1939). Therefore, the population experiences one or occasionally two aerial exposures per day during the spring portions of a tidal series, and zero or one exposure per day during the neap portions.

METHODS

At El Bajo, the *Onchidella binneyi* population is restricted to a 2-m wide strip parallel to the drift line. A 20-m long section of this strip was marked for observation. To avoid disturbing the animals' natural activities, the area was studied from its perimeters only, and animals were never removed from it. Observations were made from 5 to 21 August 1978 and from 10 to 24 May 1979.

Specimens of *Onchidella binneyi* observed on the tops and sides of rocks were considered active (WELLS [1980] followed a similar definition for limpets). The number of active animals was recorded every 30 min. Counts were begun when the falling tide first uncovered the marked area and were continued until animals were no longer observed on rock surfaces. The tidal height and time of low tide were also recorded. Nighttime observations were made using flashlights. Two independent counts were conducted simultaneously to ensure accuracy. A light-dark preference experiment showed that the slugs' movements were not affected by the flashlights.

A set of experiments was run from 13 to 19 May 1979 to determine whether the activity pattern would persist if the animals were left submerged in seawater. Three 1-L jars (16 cm tall) with screen tops were used as aquaria. Ten specimens of *Onchidella binneyi* were placed in each jar and the jars were filled with seawater to within 4 cm of the top. The water was partially changed each day but never totally drained, thus simulating a non-tidal condition. The aquaria were shaded from the sun. The number of active slugs and the time of activity were recorded periodically for the experimental and field populations simultaneously.

RESULTS

Behavior Synchronous with the Tides

Onchidella binneyi was active only at night when exposed to the air. During these activity periods the animals had a particular appearance: their mantle margins were lifted above the substrate; their eyestalks were extended and their oral lobes were swept from side to side; and

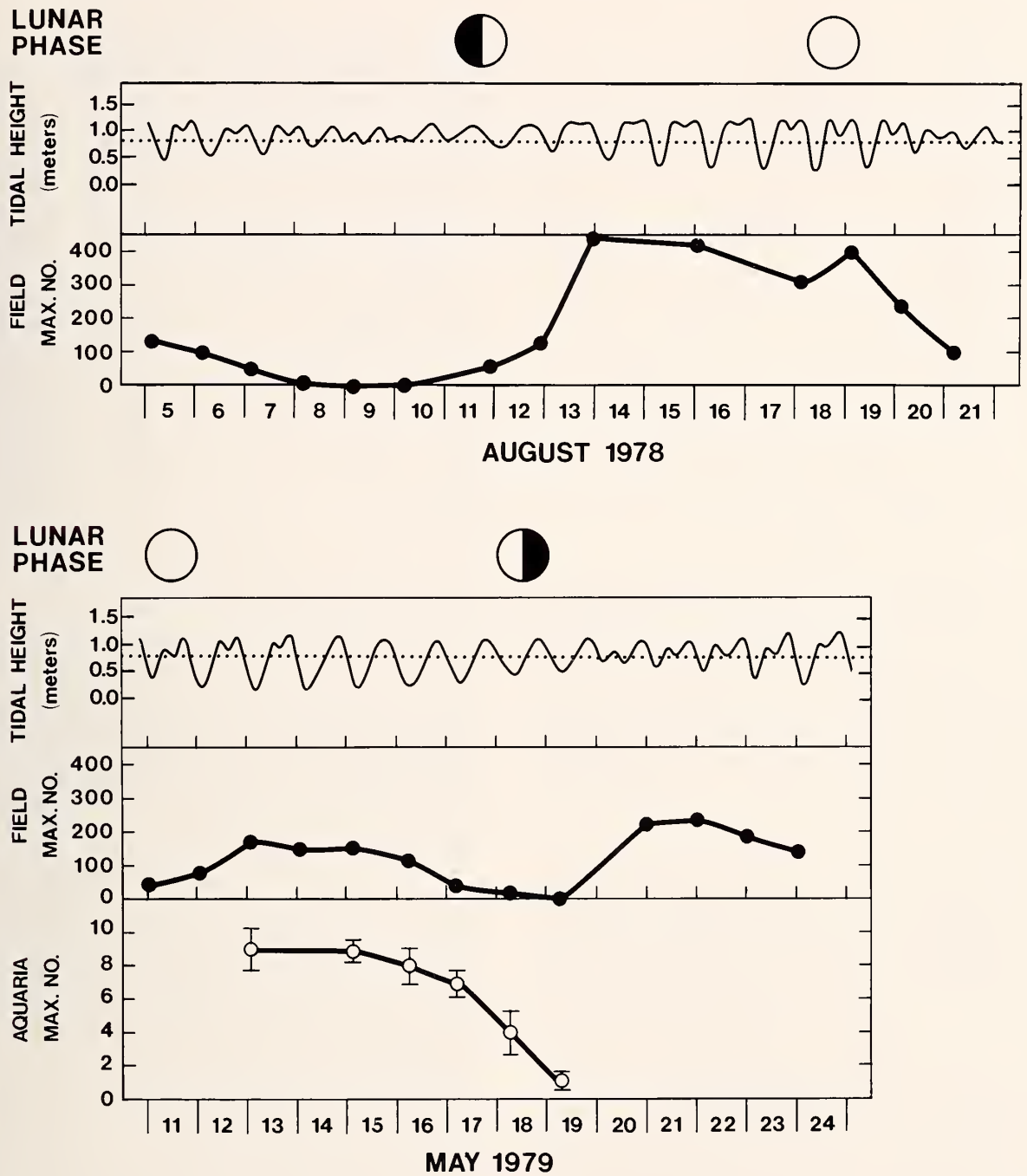

Figure 2

The intensity of nightly activity (maximum number active) is compared with the tidal amplitudes (NOAA predictions for Guaymas, Mexico) and the lunar phases for each census period. The August and May graphs both report data for the field population (closed circles). Each point represents a single night's maximum count. The May graph reports data for the experimental population in the aquaria (open circles). Each experimental point represents the mean of three replicates and includes standard error bars. The horizontal dotted lines through the tidal amplitudes depict the tidal height of the animals' position on the shore.

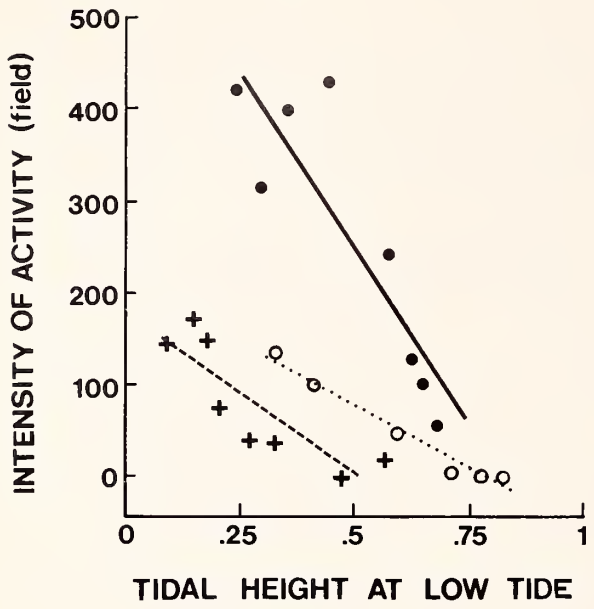

Figure 3

The relationship between the intensity of activity (maximum number active) in the field population and the predicted tidal height at low tide. Each point represents one night of the census period. Regression lines are fitted to the data points for each of three tidal series. August 5 to 10, 1978 (part of a new moon tidal series) is depicted with open circles and a dotted line (r^2 = 0.98). August 11 to 21, 1978 (part of a full moon tidal series) is depicted with closed circles and a solid line (r^2 = 0.77). May 11 to 19, 1979 (part of a full moon tidal series) is depicted with crosses and a dashed line (r^2 = 0.72).

their dorsal surfaces were flat and mantle papillae were retracted. Activities included grazing on diatom films, copulating, and moving about at an average speed of 2 cm/min (determined by measuring the distance covered during 1 h for 10 animals).

During the active periods, individual animals were observed on the upper surfaces of the rocks for durations of from 1 min to over an hour. The animals did not emerge or retreat simultaneously. Instead animals moved between active and inactive portions of the population.

The number of animals active on the surface followed a particular pattern each night. The active period began shortly after the ebbing tide uncovered the study area. The number of animals on the surface increased steadily to a maximum and then declined until all activity ceased during the hour of low tide (Figure 1).

The time of the active period progressed during a tidal series in the same manner as the tides (approximately 0.8 h each night). Maximum activity occurred an average of 1 h before low tide. The time between successive peaks of activity was not significantly different from the duration of a lunar day (24.8 h), averaging 24.6 ± 0.5 h (±SD, t-test, P = 0.5, n = 20).

The intensity of activity (maximum number of animals active each night) followed the monthly variation in the amplitude of the tides (Figure 2). These maximum numbers were inversely correlated with the tidal heights at low tide in both August and May ($r^2 \geq 0.72$, 95% confidence) (Figure 3). The data were divided into new and full moon tidal series for this analysis because they were separated by days having neap tides (August 10, May 19). These dates marked the division between fortnightly activity cycles when the moon was in the first and last quarters, respectively, and *Onchidella binneyi* was inactive.

Repeated attempts were made to find slugs during daytime ebbing tides, and when their zone was submerged. Although no surface activity was observed on these occasions, animals were found by turning over rocks adjacent to the marked study area. These slugs were inactive and huddled together in small groups. The inactive animals had their eyestalks and oral lobes retracted, their dorsal surfaces highly arched, and their mantle papillae extended, giving them a frilly appearance. Inactive slugs were never observed copulating (Webb *et al.* [1969] reported a similar finding for *Onchidella peronii*).

Behavior Independent of Tidal Cues

The daily activity cycles of *Onchidella binneyi* held in aquaria were very similar to those of the field population (Figures 1, 4). When inactive, the slugs huddled together on the bottoms of the jars, and exhibited the characteristic frilly appearance. When active, they crawled up the sides of the jars, above the waterline, and made grazing attempts on the glass with their radulae. Animals were considered active when observed at least 4 cm above the bottom of their jar.

The details of the activity cycles of the experimental group were compared to those of the field population. There was no significant difference between the mean time at which the first animals became active in the aquaria and in the field (t-test, P = 0.4, n = 18). The mean time at which the maximum activity occurred was also not significantly different between the experimental and field populations (t-test, P = 0.4, n = 18).

DISCUSSION

Onchidella is behaviorally adapted to the intertidal environment. When the slugs are submerged in seawater their lungs are inoperative and they depend upon diffusion of gases through the mantle surface. The metabolic demands of locomotion cannot be met during submergence and activity is severely limited (Fretter, 1943; Denny, 1980). Feeding excursions and sexual activities are curtailed. In addition, *Onchidella* does not have the ability to clamp tightly to rocks, and is easily dislodged by wave surge (Arey & Crozier, 1921; Marcus & Marcus, 1956). When submerged in seawater, *Onchidella* must spend its time buried under rocks. When exposed to the air, pul-

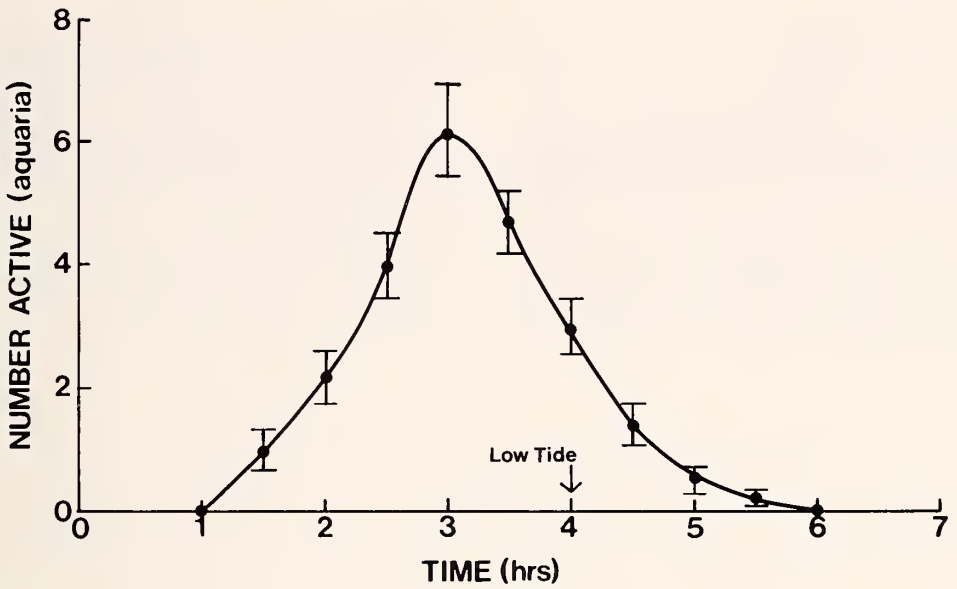

Figure 4

The mean number of active animals during six nights of activity for the experimental population of *Onchidella binneyi* held in three 1-L jars filled with seawater (10 animals per jar). Each point is the mean of three replicates for all six nights of the experiment (n = 18). The bars represent the standard errors of the mean. The arrow indicates the average time of low tide relative to the activity of the experimental population.

monary respiration supplements pallial diffusion and the slugs are able to crawl on the top surfaces of rocks where they feed on diatom films, seek mates, and copulate. However, their foraging time is limited. *Onchidella* is shell-less and subject to dehydration and loss of pulmonary capabilities if not submerged periodically (Arey & Crozier, 1921; Fretter, 1943). They will die if exposed to warm, dry air for prolonged periods. Therefore, *Onchidella* must live at a level on the shore that is alternately exposed and submerged. When the tide ebbs they must emerge, forage on rock surfaces, and return to cover before the tide rises and floods their position on the shore.

Onchidella binneyi is faced with a choice when its position on the shore is exposed to the air. The slugs can maximize their feeding rate and frequency of copulation by staying on the surfaces of rocks or they can minimize the risks of dehydration and being dislodged by waves by returning early to cover. Theoretically, the animals that would live longest and leave the most offspring would be those that emerge early and return to cover at the appropriate time to balance risks and rewards (Spight, 1982).

To optimize foraging behavior, *Onchidella binneyi* would have to match its activity to the fortnightly tidal pattern. The duration of aerial exposure of the slugs' zone changes during a tidal cycle. At neap tides, the water level either does not drop below their zone at all, or drops barely below it for up to only 4 h. At spring tides, the water level drops well below the slugs' level on the shore and exposure lasts for 6 to 8 h. As the tides progress from neap to spring, the *O. binneyi* population becomes more and more active, seemingly taking advantage of the longer exposure periods. As the tides progress from spring to neap, the population becomes less active, seemingly to avoid the risks of wave action.

The activity rhythm of *Onchidella binneyi,* with its period of a lunar day, is probably a circalunadian rhythm, as defined by Palmer (1974). The activity patterns of the *O. binneyi* population are synchronous with the tides and its nightly activity persists when left in standing seawater in aquaria. This indicates that either the population is directly cued by some other environmental factor that fluctuates in relationship with the tides, or that *O. binneyi* possesses an internal biological clock.

ACKNOWLEDGMENTS

We wish to thank Dr. R. C. Brusca of the University of Southern California for critically reading this manuscript. A sincere note of thanks to Dr. D. A. Thomson of the University of Arizona and the citizens of Loreto, whose gracious hospitality and logistic support were a great help during the field research. Thanks to Mr. and Mrs. F. Pepe whose contributions supported this work.

LITERATURE CITED

Arey, L. B. & W. J. Crozier. 1921. On the natural history of *Onchidium*. J. Exp. Zool. 32(3):443–502.

Denny, M. 1980. Locomotion: the cost of gastropod crawling. Science 208:1288–1290.

Fretter, V. 1943. Studies on the functional morphology and

embryology of *Onchidella celtica* (Forbes & Hanley) and their bearing on its relationships. J. Mar. Biol. Assoc. U.K. 25:685–720.

HIRASAKA, K. 1912. On the structure of the dorsal eye of *Onchidium*. Dobutsu Gaku Zasshi (Zool. Mag.) 24:20–35.

IRELAND, C. & D. J. FAULKNER. 1978. The defensive secretion of the opisthobranch mollusc *Onchidella binneyi*. Bioorganic Chem. 7:125–131.

MARCUS, E. & E. MARCUS. 1956. On *Onchidella indolens* (Gould, 1852). Bol. Inst. Oceanogr. S. Paulo 5(1–2):87–94.

PALMER, J. D. 1974. Biological clocks in marine organisms: the control of physiological and behavioral tidal rhythms. Wiley & Sons: New York. 173 pp.

RICKETTS, E. F. & J. CALVIN. 1939. Between Pacific tides. Stanford Univ. Press: Stanford, Calif. 614 pp.

SPIGHT, T. M. 1982. Risk, reward, and duration of feeding excursions by a marine snail. Veliger 24(4):302–308.

WATSON, H. 1925. The South African species of the molluscan genus *Onchidella*. Ann. So. Afr. Mus. 20(4):237–308.

WEBB, M., L. G. MOODLEY & A. S. THANDAR. 1969. The copulatory mechanism in *Onchidium peronii*. So. Afr. J. Sci. 65(4):107–112.

WELLS, R. A. 1980. Activity pattern as a mechanism of predator avoidance in two species of acmaeid limpet. J. Exp. Mar. Biol. Ecol. 48(2):151–168.